

Dynamic Bone Remodeling in Later Pleistocene Fossil Hominids

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ABSTRACT Histomorphometric analysis of femoral and tibial diaphyseal fragments from seven Late Archaic and three Early Modern humans are compared with those of the Pecos, a pre-Columbian Native American population. The ten samples, from Broken Hill (EM-793), Shanidar 2, 3, 4, 5, and 6, Tabun 1, and Skhul 3, 6, and 7, provide age-at-death results consistent with earlier estimates for most individuals. The Pleistocene groups exhibit less bone turnover and smaller osteons than Recent populations. Resorption and formation were both coupled and balanced in these Pleistocene populations, but the overall vigor of individual cells from both the osteoclast and osteoblast cell lines was less than in Recent populations. Thus the greater bone mass in Later Pleistocene members of the genus *Homo* is not the result of higher levels of bone turnover, at least among adults. © 1996 Wiley-Liss, Inc.

Using both external osteometrics and assessments of diaphyseal cross-sectional geometry (e.g., Twisselmann, 1961; Endo and Kimura, 1970; Trinkaus, 1976, 1983; Lovejoy and Trinkaus, 1980; Lovejoy, 1982; Trinkaus and Ruff, 1989; Kimura and Takahashi, 1992; Ruff et al., 1993a), an increasing volume of research has documented significant changes in lower limb diaphyseal robustness through Pleistocene genus *Homo*. An elevated level of femoral and tibial robustness persisted through Archaic members of the genus *Homo* and into Early Modern humans of the Late Pleistocene, being evident in both immature and mature Archaic members of the genus *Homo* (Ruff et al., 1993, 1994). This robustness then reduced gradually through Holocene human populations (Ruff et al., 1993).

Interpretations of this pattern of lower limb diaphyseal robustness have assumed that the relatively larger amount of diaphyseal cortical bone and its biomechanically more effective distribution around the di-

aphyseal neutral axis reflect higher levels of bone deposition and/or lower levels of resorption in response to habitually higher strain levels; those elevated strain levels in turn are assumed to have resulted from elevated and/or prolonged locomotor behavior (e.g., Ruff et al., 1993). This interpretation has been supported by experimental research on bony hypertrophy and atrophy in response to mechanical stimuli across modern mammals (including humans) (see Trinkaus et al., 1994, and Martin and Burr, 1989, for a review) as well as high levels of humeral diaphyseal asymmetry seen in Recent humans with pronounced unilateral upper limb activity levels (baseball and tennis athletes [King et al., 1969; Jones et al., 1977; Trinkaus et al., 1994]) and in Neandertals with

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and without unilateral upper limb trauma (Trinkaus et al., 1994).

Nonetheless, there have been suggestions (e.g., Keith, 1928; Brothwell, 1975; Kennedy, 1985; Smith et al., 1989) that the robustness characteristic of the Neandertals and other Archaic members of the genus *Homo*, as reflected in their large external bone dimensions and thick diaphyseal cortical bone relative to body size in contrast to those of modern humans, might have been produced by differences in their endocrinological or genetic control of bone remodeling, independent of habitual strain levels on those bones. The need to invoke such physiological contrasts to account for archaic *Homo* robustness has been questioned through asymmetry studies, in which it is assumed that any such effects on diaphyseal robusticity would be systemic and hence bilaterally symmetrical (Trinkaus et al., 1994). However, the histological processes responsible for this robustness remain unknown, and it remains possible that the mechanisms and/or rates of bone remodeling in Pleistocene humans differed in some fundamental way from those of modern humans.

Techniques are currently available to measure the dynamics of bone turnover even when vital stains, such as tetracycline, have not been used (Wu et al., 1970; Frost, 1987a,b). Analysis of relevant bone remodeling variables, such as activation frequency and bone formation rates, allows the comparison of skeletal dynamics in fossil hominids with those of more modern humans. We therefore analyzed an available sample of Late Archaic (late Middle to early Late Pleistocene) and Early Modern (early Late Pleistocene) human femoral and tibial diaphyseal cortical bone histological sections, comparing them to those of a prehistoric to early historic Amerindian sample from Pecos Pueblo, to assess the nature of Pleistocene human bone remodeling dynamics relative to those of Recent humans.

MATERIALS AND METHODS

Fossil remains

The paleontological sample is relatively small given the invasive nature of any histological analysis. However, it has been possi-

ble to obtain lower limb diaphyseal samples (femoral in all cases except Shanidar 2) from eight late archaic humans from the sites of Broken Hill, Kebara, Shanidar and Tabun and four early modern humans from the site of Skhul.¹ All but one of these specimens (Broken Hill EM-793) derive from Near Eastern Middle Paleolithic deposits.

The Broken Hill (or Kabwe) EM-793 specimen consists of a femoral midshaft section 121.5 mm long, of indeterminate side, since proximal vs. distal cannot be assessed even though medial vs. lateral can be determined from the linea aspera morphology (Clark et al., 1968). The histological sample is from a full cross section of the femoral shaft, which had previously been sawed off the shaft section in the original analysis (Fig. 1). As with all of the Broken Hill specimens, the bone is completely impregnated with lead and zinc, and has excellent preservation. None of the Broken Hill fossil hominid remains has secure stratigraphic associations or accurate geological ages (Hrdlička, 1930; Clark et al., 1950). However, assuming that the Broken Hill EM-793 femur was associated with the other cranial and postcranial remains from the locality, as is supported by its geochemistry (Clark et al., 1968), and that these hominid remains were associated with the recovered faunal remains, the combination of archaic morphology in (especially) the Broken Hill 1 cranium and the presence of extinct Middle Pleistocene species in the faunal sample suggests a late Middle Pleistocene geological age, probably in the vicinity of 200–300 ka B.P. (Klein, 1973).

The Tabun 1 specimen consists of a largely complete associated skeleton, which retains an intact but crushed right femur plus the distal epiphysis and shaft fragments of the left femur (McCown and Keith, 1939). From the left femoral shaft fragments, a piece was

¹The Kebara sample consists of fragments of the eroded, leached and crushed femoral diaphysis of Kebara 2. Even though we were able to obtain histological sections of these fragments, the individual pieces are too small to provide useful data. In addition, the sample from one of the Skhul specimens, Skhul 5, produced a totally opaque histological section, which was unreadable with either transmitted or reflected light. As a result, the final analyzed sample consists of seven Late Archaic humans and three Early Modern humans.

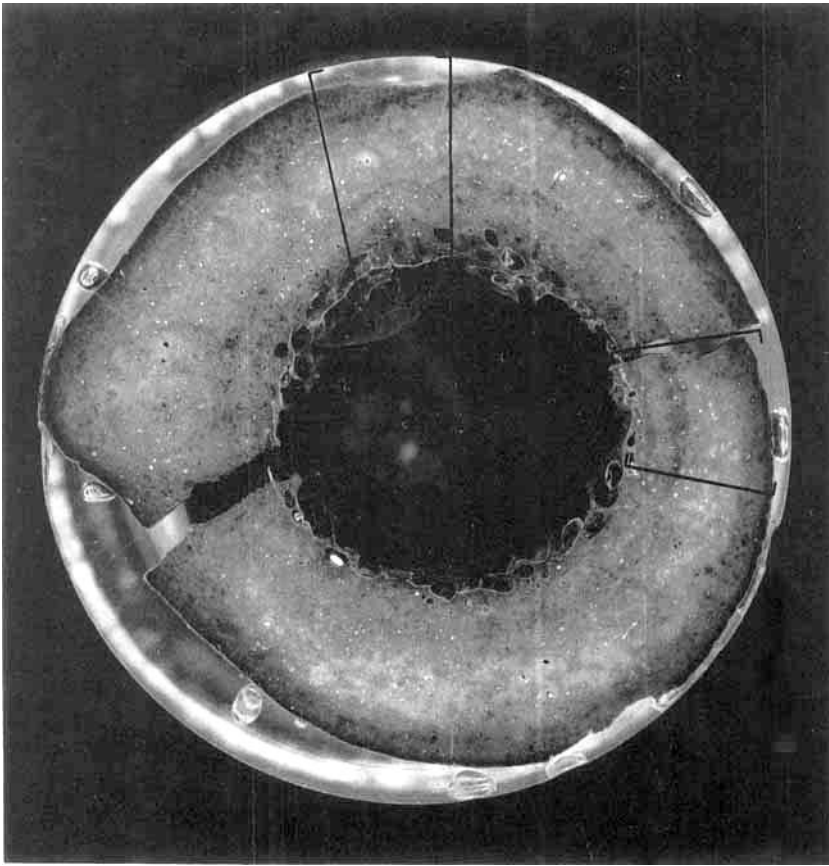


Fig. 1. Complete midshaft femoral cross section from the Broken Hill (EM-793) specimen embedded in methylmethacrylate and surface polished. Histomorphometric measurements were made in the regions denoted by the brackets (anterior and lateral). Actual magnification = $2.55\times$.

chosen whose surface and cross-sectional morphology appeared to most closely approximate that of the right femoral midshaft without any trace of the dorsal muscular attachments; it probably derived from the distal third of the shaft but was clearly separate from the distal epiphysis.

The Tabun 1 partial skeleton most likely derives from Layer C of Tabun Cave, as originally concluded by Garrod and Bate (1937) and McCown and Keith (1939). It is possible, as suggested by Garrod and Bate, that it was an intrusive burial from Layer B or, as suggested by Jelinek (1992), that it derives from the higher portion of Layer D close to the wall of the shelter where the skeleton was discovered. However, since the Tabun 4 and 5 distal radius and hamate clearly de-

rive from the Tabun 1 skeleton (Trinkaus, pers. observ.) and are securely associated with Layer C, it is most likely that the Tabun 1 skeleton is of the same geological age as Layer C. Even though Tabun Layer C has been assigned geological ages from the early last glacial (Jelinek, 1982) to the late Middle Pleistocene (Mercier, 1992), it is most likely that it dates to the middle of the last interglacial, ca. 100 ka B.P. (Grün et al., 1991; McDermott et al., 1993).

The Shanidar samples all derive from associated skeletons of Late Archaic humans, from the middle (Shanidar 2, 4 and 6) and upper (Shanidar 3 and 5) levels of the Middle Paleolithic Layer D in Shanidar Cave (Trinkaus, 1983). The Shanidar 4, 5 and 6 samples are from pieces of femoral diaphysis which

could not be glued onto the reconstructed femoral diaphyses, and the Shanidar 3 piece is an isolated piece of femoral diaphyseal cortical bone. All were judged, based on their morphology and compared to other portions of their femora (for Shanidar 4, 5 and 6), to be from the middle half of the diaphysis and well separated from the linea aspera. The Shanidar 2 sample derives from the proximal diaphysis of its otherwise largely complete left tibia and consists of pieces which could not be glued onto the bone.

The geological age of the Shanidar Middle Paleolithic deposits remains uncertain, since only radiocarbon techniques have been applied to the site (Vogel and Waterbolk, 1963) and those have provided only minimum ages ca. 40–50 ka B.P. It appears most likely, using both archeological and cranial morphological considerations (Trinkaus, 1991), that the earlier samples (Shanidar 2, 4 and 6) date to the middle of the last interglacial (± 100 ka B.P.) and that the later specimens (Shanidar 3 and 5) derive from the early last glacial (± 50 –75 ka B.P.).

The cranio-facially robust Early Modern human Skhul sample, which is morphologically distinct from the Near Eastern Late Archaic humans from Amud, Kebara, Shanidar and Tabun (Vandermeersch, 1981; Trinkaus, 1983, 1993), consists of a series of partial skeletons (McCown and Keith, 1939). From these, useable femoral diaphyseal samples were obtained from Skhul 3, 6 and 7. Each sample consisted of approximately 4 mm³ of anterior femoral midshaft cortical bone, removed from the reconstructed femoral diaphyses. Each was taken adjacent to a plaster-filled gap in the shaft, to minimize damage to the already incomplete diaphyses. Given this technique for sampling these femora, the histological samples for these individuals were the smallest available.

The Skhul sample derives from Layer B of the (now fully excavated) terrace deposits at Mughareh es-Skhul. The associated fauna from these deposits has been uranium-series and ESR dated to both ca. 80–100 ka B.P. and 40–50 ka B.P. (Stringer et al., 1989; McDermott et al., 1993). These fossils could therefore derive from the middle of the last interglacial and/or the early last glacial, with a reasonable age range of 40–100 ka B.P.

The Late Archaic sample consists of two females (Tabun 1 and Shanidar 6), four males (Shanidar 2, 3, 4 and 5) and one specimen of indeterminate sex (Broken Hill EM-793). Of these, two (Tabun 1 and Shanidar 4) were sexed using the pelvis, and others were assigned based on overall size considerations (McCown and Keith, 1939; Trinkaus, 1983). The Skhul 3 and 6 were considered male by McCown and Keith (1939) and Skhul 7 designated female by them; all of these assessments are based on overall size alone. Therefore, in the comparisons of the fossil samples to the sex-specific samples from Pecos Pueblo (see below), it should be kept in mind that there is probably a slight male bias in the paleontological sample.

Recent humans

The results from the histological analysis of these fossil femoral and tibial specimens were compared to 55 femoral samples of males and females from Pecos Pueblo (Hooton, 1930). The sample employed here was previously described by Ruff and Hayes (1983) and histologically analyzed by Burr et al. (1990). Given the presence of Late Archaic and Early Modern humans in the fossil sample and sufficient numbers of males and females in the Recent human sample, the results were analyzed comparing the Late Archaic sample, the Early Modern human sample and the pooled fossil sample to the male and female Pecos Pueblo samples.

Ages-at-death: Current estimates

Histomorphometric assessments of age determined in this paper were compared to traditional macroscopic age indicators, or previous histomorphometric age assessments.

The ages of the Shanidar 3, 4, 5 and 6 individuals were previously based primarily on dental occlusal attrition (moderate for Shanidar 6 and marked for the others) plus femoral histomorphometric assessments (Thompson and Trinkaus, 1981; Trinkaus, 1983; Trinkaus and Thompson, 1987). In addition, portions of the pubic symphyseal and auricular surfaces are preserved for Shanidar 3, and cranial vault morphology, including both cranial suture morphology and the cross sections of the tables and diploë, are

TABLE 1. Summary of age-at-death calculations

Specimen	Morphological age-at-death estimate ¹	Previous histologically calculated age-at-death ²	Calculated age-at-death	Sex
Late Archaic				
Broken Hill (EM-793)	N/A	N/A	51	?
Shanidar 2 ³	20–30	N/A	55	M
Shanidar 3	40–50	41	42	M
Shanidar 4	30–45	34	33	M
Shanidar 5	35–50	40	34	M
Shanidar 6	20–35	24	25	F
Tabun 1	25–30	N/A	30	F
Early Modern				
Skhul 3	Adult	N/A	18	M
Skhul 6	25–35	N/A	28	M?
Skhul 7	30–40	N/A	32	F?

¹ McCown and Keith, 1939; Trinkaus, 1983, pers. observ.; Loth, 1992.

² Trinkaus and Thompson, 1987.

³ Proximal tibia.

available for Shanidar 4 and 5. All of these macroscopic indicators suggest relatively advanced ages for Shanidar 3, 4 and 5, and a younger age for Shanidar 6. The previous histomorphometric assessments (Table 1) show a high degree of concordance with these estimates. The age of Shanidar 2 was previously assessed using the occlusal attrition of its essentially complete dentition plus its cranial vault morphology. Both of these indicate a young adult age, and the dental attrition in particular indicates an age below that of Shanidar 6; by comparison with the mid-20s histomorphometric age for Shanidar 6 and the minimal wear on the M3s of Shanidar 2, a morphological age in the early 20s is indicated.

The age of Tabun 1 was originally estimated at "about 30 years" by McCown and Keith (1939), an age that fits with our current assessments of Neandertal dental attrition rates and the amount of wear on the almost complete Tabun 1 dentition. Loth (1992), however, based on sternal rib remodeling patterns (Iscan et al., 1985), assigned a younger age, in the early 20s, to this individual.

The Broken Hill EM-793 and Skhul 3 specimens include only a femoral shaft and portions of femur, tibia and fibula respectively. Consequently, there are no macroscopic age indicators preserved on them.

The ages-at-death of the Skhul specimens have not been systematically reviewed since

the work of McCown and Keith (1939). They assigned ages of 30–35 years to Skhul 6 and 35–40 years to Skhul 7, apparently on the basis of the degree of wear on their dentitions. The moderate degrees of wear on their teeth, combined with the current absence of alternative analyses to assess rates and patterns of dental attrition in the Near Eastern Early Modern human sample, suggest that these ranges should probably be extended downward, to 25–35 years and 30–40 years respectively.

The ages-at-death of the Pecos Pueblo sample were determined using traditional macroscopic techniques: epiphyseal union, dental attrition, pubic symphyseal morphology, cranial suture morphology, and vertebral osteophytosis, as applicable for the age group in question (Ruff, 1991). These individuals were only assigned to a decade of life, given the approximate nature of some of these age indicators.

Sample preparation

The paleontological sample consisted of 24 histologically useable bone fragments, 22 samples of femoral diaphyseal cortical bone and two samples of tibial diaphyseal cortical bone. Access to specimens is largely determined by the presence of fragments that do not form part of an integrated reconstructed shaft. Only limited control therefore could be exercised over sample location. Samples from 10 individuals were variably located

as to position on the original diaphysis (see above), but it is known (for the Skhul specimens) or estimated based on the morphology (for the Shanidar and Tabun femoral pieces) that they should derive from the anterior, medial or lateral diaphysis in the middle half of the shaft. Given the complete cross section available for the Broken Hill specimen, it was sampled histologically in two places, along the anterior and (probably) the lateral diaphysis (Fig. 1).² Also, because all except the Broken Hill piece consisted of subperiosteal cortical bone without a clear endocortical margin, only the Broken Hill specimen provides histological data for the full cortical thickness of the diaphysis. All except the lead and zinc impregnated Broken Hill specimen consisted of fragile and leached cortical bone, impossible to section or polish without embedding in a plastic matrix. They were therefore dried in a series of graded alcohols (70%, 80%, 90%, 100%), infiltrated and finally embedded in DDK-plast (Delaware Diamond Knives, Wilmington, DE). The surface of the block was polished using alumina in water suspension to a final polish with 0.3 μ alumina.

Measurements

The polished blocks were examined at 125 \times magnification under incident light using a Nikon Optiphot microscope with Nomarski optics. Osteonal dimensions were digitized onto a Summagraphics digitizing tablet using a mouse with an LED projected through a drawing tube into the field of view in the microscope. Data were collected with Bioquant image analysis software (R & M Biometrics, Nashville, TN). Table 2 summarizes the measured and derived variables.

Several polished blocks were measured for each fossil specimen when the quantity of mineralized bone tissue and its state of preservation made this possible (Table 3). If lamellar borders were clear, the section was read. For all sections, the entire area of each sample was measured, except for the cross section of Broken Hill discussed above. An

average of 30.45 mm² of tissue area was measured for each Neandertal individual. Properties of multiply sampled individuals were averaged in all subsequent analyses.

Histomorphometric age calculations

Age-at-death calculations were performed following the method established by Thompson (1979; Thompson and Galvin, 1983). For each bone fragment of each individual, secondary osteon number (N.On) and area (On.Ar) were determined. Partial osteons were found along the broken edges of the sections. If these had been ignored, the osteon population density (OPD) and percent osteonal bone would have been underestimated. To correct for this, the number of partial osteons was multiplied by the mean area of whole secondary osteons, used as an estimate of the area these osteons would have occupied had they been complete. The summed areas of whole and partial osteons were used to calculate percent osteonal bone (On.B). The On.B was used to calculate age according to the equation: $y(\text{age}) = 101.9 * (\text{On.B}/100) + 6.667$, an equation based on Recent Euroamericans originally for forensic purposes. This is the equation previously employed by Trinkaus and Thompson (1987) in their calculation of ages-at-death for the Shanidar specimens; it provided estimates that were consistent with traditional macroscopic techniques. For tibial data from Shanidar 2, Thompson's (1979) regression equation for the left tibia of males was used to calculate age: $y(\text{age}) = 75.93(\text{On.B}/100) + 25.966$.

Inconsistencies between histomorphometric ages calculated using this technique and either known ages or ages estimated from macroscopic aging techniques (e.g., Thompson and Gunness-Hey, 1981; Stout, 1992; Aiello and Molleson, 1993), as well as questions regarding the interpopulational accuracy of many aging techniques as applied to adult skeletal remains (Jackes, 1992), have been noted. However, the close correspondence between the histomorphometric age determinations for the Shanidar remains and other age indicators (Trinkaus, 1983; Trinkaus and Thompson, 1987), plus the use of similar macroscopic aging techniques for both the fossil and Pecos remains, suggest

²Side determination on this specimen is difficult. Because it is only a piece from the femoral midshaft, proximal and distal are indeterminate. Our best estimation is that this cortex is lateral, although there is a possibility it is medial.

TABLE 2. Measured and derived histomorphometric parameters

Parameters	Measured		Description	Derived	
	Code	Unit		Parameters	Code Unit Formula
Bone area	B.Ar	μm^2	Entire area excluding marrow cavity	Osteonal mean wall thickness	W.Wi μm^2 $(\text{On.Ar} - \text{Ca.Ar})/(\text{On.Pm} + \text{Ca.Pm})/2$
Osteon area	On.Ar	μm^2	Mean area of whole secondary osteons with complete canals	Percent osteonal bone	On.B %
Osteon perimeter	On.Pm	μm	Mean perimeter of the cement line of whole secondary osteons	Porosity	Po %
Haversian canal area	Ca.Ar	μm^2	Mean canal area of whole secondary osteons	Osteonal refilling	On.Rf %
Haversian canal perimeter	Ca.Pm	μm	Mean perimeter of the Haversian canal of whole secondary osteons	Osteon population density	OPD no./mm^2
Pore area	Po.Ar	μm^2	Total area of all Haversian and non-Haversian canals	Activation frequency	Ac.F $\text{no./mm}^2/\text{yr}$
Number of osteons	N.On	no.	Number of whole secondary osteons	Bone formation rate	BFR %/yr
Osteon fragments	N.On.Fg	no.	Osteon segments with a definite curvature, lamellar pattern and cement line, but no Haversian canal		

¹ Accumulated osteon creations (AOC) is derived from OPD according to equation 2.

² Where On.Ar is in mm^2 .

TABLE 3. *Histomorphometric parameters of Pleistocene specimens*¹

Specimen	On.Ar (Mean µm ²)	On.Pm (Mean µm)	Ca.Ar (Mean µm ²)	Ca.Pm (Mean µm)	W.Wi (µm)	On.B (%)	Porosity (%)	On.Rf (%)	OPD (/mm ²)	Age at death (yr)	Total B.Ar (mm ²)
Late Archaic											
Broken Hill											
Brkhl?Fa	39167.80	727.17	3840.53	215.59	74.94	35.20	6.94	90.19	10.03	42.55	28.53
Brkhl?Fb	33387.14	666.06	2487.20	171.54	73.78	51.84	4.83	92.55	17.77	59.50	39.17
Mean	36277.47	696.61	3163.87	193.56	74.36	43.52	5.89	91.37	13.90	51.02	33.85
SE	2044.77	21.61	478.47	15.57	0.41	5.88	0.75	0.83	2.74	6.00	3.76
Shanidar 2											
LTa	34814.10	676.91	2157.32	168.52	77.26	34.58	4.00	93.80	11.36	52.22	13.29
LTb	41042.31	739.53	2890.26	193.16	81.81	44.30	8.28	92.96	12.62	59.60	23.62
LTc	36869.72	705.54	2559.77	181.39	77.37	36.23	5.35	93.06	10.39	53.48	26.46
Mean	37575.38	707.33	2535.78	181.02	78.81	38.37	5.88	93.27	11.46	55.10	21.12
SE	1496.00	14.78	173.03	5.81	1.22	2.45	1.03	0.22	0.53	3.22	3.27
Shanidar 3											
?Fa	17725.87	486.23	1079.00	115.21	55.36	34.63	5.73	93.91	24.29	41.96	109.24
Shanidar 4											
LFa	30108.12	640.10	3197.52	201.13	63.98	20.16	5.71	89.38	7.29	27.22	25.39
LFb	33382.09	657.55	3297.24	198.08	70.32	27.13	5.11	90.12	9.20	34.32	25.10
LFc	24221.58	575.70	1699.53	141.11	62.84	26.95	4.99	92.98	13.27	34.14	94.11
?Fb	31358.85	665.75	3776.78	201.09	63.64	27.29	6.60	87.96	11.60	34.49	19.32
Mean	29767.66	634.77	2992.77	185.35	65.20	25.38	5.60	90.11	10.34	32.54	40.98
SE	1704.24	17.67	389.05	12.79	1.49	1.51	0.28	0.91	1.14	1.54	15.39
Shanidar 5											
?Fa	23323.37	557.97	1556.65	140.32	62.34	22.33	8.00	93.33	11.52	29.43	23.08
?Fb	24499.61	580.38	1317.29	130.25	65.24	31.70	2.29	94.62	15.62	38.98	8.96
?Fc	25054.33	582.09	1470.31	133.86	65.88	27.71	4.64	94.13	13.40	34.91	23.96
Mean	24292.44	573.48	1448.08	134.81	64.49	27.25	4.98	94.03	13.51	34.44	18.67
SE	416.69	6.34	57.14	2.40	0.89	2.22	1.35	0.31	0.97	2.26	3.97
Shanidar 6											
LFa	22243.76	547.37	1389.49	132.18	61.38	11.44	4.19	93.75	5.14	18.33	24.51
LFb	26133.97	595.01	1166.42	123.60	69.49	26.41	3.97	95.54	13.47	33.58	14.84
LFc	26048.10	586.34	1579.58	138.13	67.55	28.75	5.30	93.94	15.13	35.97	87.17
RFa	21851.66	560.91	1861.42	154.27	55.90	10.66	2.57	91.48	5.91	17.54	10.66
RFb	23395.92	573.49	1177.44	124.79	63.64	18.93	2.32	94.97	9.48	25.97	8.65
RFc	18240.95	505.18	1158.64	127.88	53.97	14.10	2.99	93.65	10.10	21.05	6.34
RFd	23321.97	580.39	1212.38	121.62	62.99	18.87	2.39	94.80	11.12	25.90	16.19
Mean	23033.76	564.10	1363.62	131.78	62.13	18.45	3.39	94.02	10.05	25.48	24.05
SE	946.58	10.66	94.06	3.99	1.98	2.47	0.39	0.46	1.28	2.35	9.96
Tabun											
LFa	35327.50	682.95	2621.71	180.36	75.77	25.91	3.88	92.58	9.55	33.08	55.62
LFb	24643.69	571.47	1988.51	161.50	61.82	19.78	2.85	91.93	9.03	26.83	63.79
Mean	29985.60	627.21	2305.11	170.93	68.80	22.85	3.37	92.26	9.29	29.96	59.71
SE	3777.30	39.41	223.87	6.67	4.93	2.17	0.36	0.23	0.18	2.21	2.89
Early Modern											
Skhul 3											
LFa	16293.57	466.94	1589.10	146.94	47.91	11.33	3.24	90.25	8.02	18.22	1.87
Skhul 6											
RFa	39287.42	756.00	3190.18	213.89	74.44	20.52	3.09	91.88	5.70	27.59	4.21
Skhul 7											
LFa	22851.36	545.42	1456.14	139.03	62.52	25.08	3.46	93.63	13.61	32.23	7.20

¹ L = left, R = right; F = femur, T = tibia; a, b, or c = individual section indicators; ? = unknown

that any biases inherent in the use of these aging techniques are likely to be consistent across the fossil and Recent human samples employed here.³

³Even though there have been suggestions that Late Archaic humans may have matured more rapidly than living humans, and hence had generally abbreviated life cycle segments (e.g., Wolpoff, 1979; Dean et al., 1986; see Trinkaus and Tompkins, 1990), current data on relative dental development (Tompkins, 1991) indicate that Late Archaic and Early Modern human dental development rates and patterns fall well within Recent human ranges of variation, implying similar life history segment lengths.

Calculation of dynamic bone remodeling

Calculation of activation frequency and bone formation rate used the method proposed by Frost (1987a,b) and recently expanded upon by Stout and Paine (1994). The method is based upon a measurement of the total number of intact and fragmentary osteons, and an estimation of the number of osteons that may have been "remodeled out" of the bone. Over time, as the number of osteons inevitably increases as bone is re-

modeled, the total visible osteon creations will reach an asymptote when each new osteon removes an old osteon. This asymptote can be calculated by

$$\text{OPD asymptote} = k(D_h^2)^{-1} \quad (1)$$

where k is a constant and D_h is the diameter of the Haversian system (i.e., osteon). It is used to define a scaling operator that, when multiplied by OPD, gives the total (visible and removed) accumulated osteon creations (AOC) ($\text{AOC} = \beta \times \text{OPD}$). Beta is defined as

$$\beta = (1 - \alpha^{3.5})^{-1} \quad (2)$$

where $\alpha = \text{OPD}/\text{OPD asymptote}$. The net osteonal remodeling (BR_h) over an individual's lifetime then can be estimated by

$$\text{BR}_h = \text{AOC} \times \text{On.Ar} \quad (3)$$

where $\text{On.Ar} = \text{mean osteon area}$.

Frost's method originally was developed using values from rib cross sections. To calculate the OPD asymptote it is necessary to find the value of k , a constant which is a packing factor that corrects for the fact that a region of bone may actually contain more intact and fragmentary osteons than predicted by a theoretical distribution (Frost, 1987a; Stout and Paine, 1994). To adapt the equations to the femur we used $k = 1.38$, to give an asymptote close to 30 osteons/mm², which can be shown to be closer to the correct value for the femur than the value used for the rib ($k = 1.70$).

The value for the asymptote (30 osteons/mm²) is based on data from Kerley (1965), who presented evidence showing an asymptote for osteons (150) and osteon fragments (100) over four fields collected from each cortex of the femoral midshaft. The total field area analyzed by Kerley, after correction for his actual field size (Kerley and Ubelaker, 1978), was 8.24 mm² (four circular fields of 1.62 mm diameter each). The average OPD asymptote for the femur was about 250 osteons/8.24 mm² or 30.34 osteons/mm². We have accepted 30 osteons/mm² as the best available estimate for the OPD asymptote.

When the missing osteons have been estimated, activation frequency (Ac.F) and bone

formation rate (BFR) can be calculated using formulae from Wu et al. (1970):

$$\text{Relative Ac.F} = \text{AOC}/\text{age} \quad (4)$$

$$\text{Relative BFR} = \text{Ac.F} \times \text{On.Ar} \times 100 \quad (5)$$

where On.Ar is in mm², and age is the mid-range of the macroscopic age estimate (Table 1).

The chronological age of an individual exceeds the mean tissue age of the compact bone because of drifts that occur during growth and because of bone turnover as a consequence of remodeling processes occurring throughout life. Based on fluorochrome labeling studies, Wu et al. (1970) calculated an adjustment of 12.5 years for the middle of the sixth rib to account for the effective "birth" of the compact bone. The value for the femur is unknown, and data needed to calculate the effective age are not available. There is no reason to believe that it will be the same as for rib. Regardless of the exact birth age this value is a constant, so we have not adjusted chronological age to account for the mean tissue age in calculating relative Ac.F. This makes Ac.F and BFR slightly smaller than the real values, but maintains internal consistency and comparability among all the archeological samples.

Because only intact osteons were counted for the Pecos sample, relative Ac.F and relative BFR were computed using only whole secondary osteons and ignoring osteon fragments. This reduces values for Ac.F and BFR from actual values that could be computed if fluorochrome labeled bone sections were available, but permits a direct comparison of Ac.F and BFR between Recent and Late Pleistocene populations.

Data analysis

Because of the small sample size, histologic and bone remodeling parameters from Late Archaic and Early Modern populations were compared to each other using nonparametric Mann-Whitney U tests. These later Pleistocene populations then were compared both separately, and by pooling Late Archaic with Early Modern samples, to males and females of the Pecos population using Kruskal-Wallis one-way ANOVA. When sig-

nificant differences were detected among the Archaic, Early Modern and Recent groups, the groups were compared pairwise using Dunn's nonparametric multiple comparison tests for post-hoc analysis. All analyses compared the two Pleistocene hominid samples with means for age-matched Pecos individuals. Individuals in the Pecos population older than 50 years were not included in the comparison.

RESULTS

Age-at-death estimation

The ages-at-death estimated from the femoral histology show a high degree of concordance with those previously estimated for four of the Shanidar individuals, and with the previous macroscopic assessments of the ages of the seven individuals preserving such age indicators (Table 1). The main differences are the slightly lower age estimation for Shanidar 5, the placement of the Skhul 6 and 7 individuals below the age ranges estimated by McCown and Keith (1939) but within the younger ranges proposed here, and the placement of Tabun 1 at the upper end of the previously estimated range (identical to the "about 30" proposed by McCown and Keith).

The one exception is the age-at-death estimated for Shanidar 2 of ca. 55 years. This value is well above the full range of 20–30 years and the more probable range of 20–25 years based on the very modest wear on the dentition. Because Shanidar 2 was discovered as an isolated associated skeleton, it is unlikely that the remains of two individuals are mixed.

The accumulation of osteons over time is highly correlated to age. Regressions of OPD (using whole and fragmentary secondary osteons) on macroscopically estimated age for the Pleistocene hominid sample, exclusive of Shanidar 2, show a significant correlation between the two (Fig. 2; $r^2 = 0.62$, $P < 0.05$). Calculating age for Shanidar 2 from the regression equation (generated without Shanidar 2) gives an age for this individual of 34 years. This is more consistent with the macroscopic age estimates for this hominid. However, using a regression of osteon density on age derived from femoral data may

not apply accurately to age estimates from tibial morphology. Stout (1984) has found that OPDs in the tibia are significantly lower than those for the femur, rib and humerus of the same individual. Thompson's (1979) regression equation for estimating age from the tibia is different than that for the femur, implying differences in femoral and tibial bone turnover rates and their relationship to age.

Interestingly, the Broken Hill EM-793 specimen provides one of the highest known age-at-death estimates for an Archaic human. It is approached only by age estimates in the fifth to sixth decades for the Neanderthal 1 and La Ferrassie 1 specimens and a few other Neandertals with extensively worn dentitions (but not more worn than those of Shanidar 3, 4 and 5, which provide much lower histomorphometric ages) (Trinkaus and Thompson, 1987; Table 1).

As a result, the total fossil sample has a calculated age range of 18 to 51 years, with the Late Archaic sample ranging from 25 to 51 years and the Early Modern sample ranging from 18 to 32 years. None of these is geriatric, and therefore they are compared only to Pecos Pueblo individuals below 50 years. Because Ac.F and BFR were calculated using age, regressions of these variables on age were not done.

Comparison of Archaic and Early Modern humans

In general, the values for measured and derived histologic and remodeling parameters in the Pleistocene samples show remarkable consistency across the fossil groups, particularly considering the geographic, temporal, gender, age and sample location variations within the study population (Tables 4 and 5). No statistically significant differences were detected between Late Archaic and Early Modern samples, although the small number of histological samples available for analysis in each of these groups makes the power of the statistical treatment low, increasing the possibility for Type II error. The small differences between Late Archaic and Early Modern populations can all be attributed to the younger age-at-death of individuals within the Early Modern population (26.01 ± 3.36 years vs.

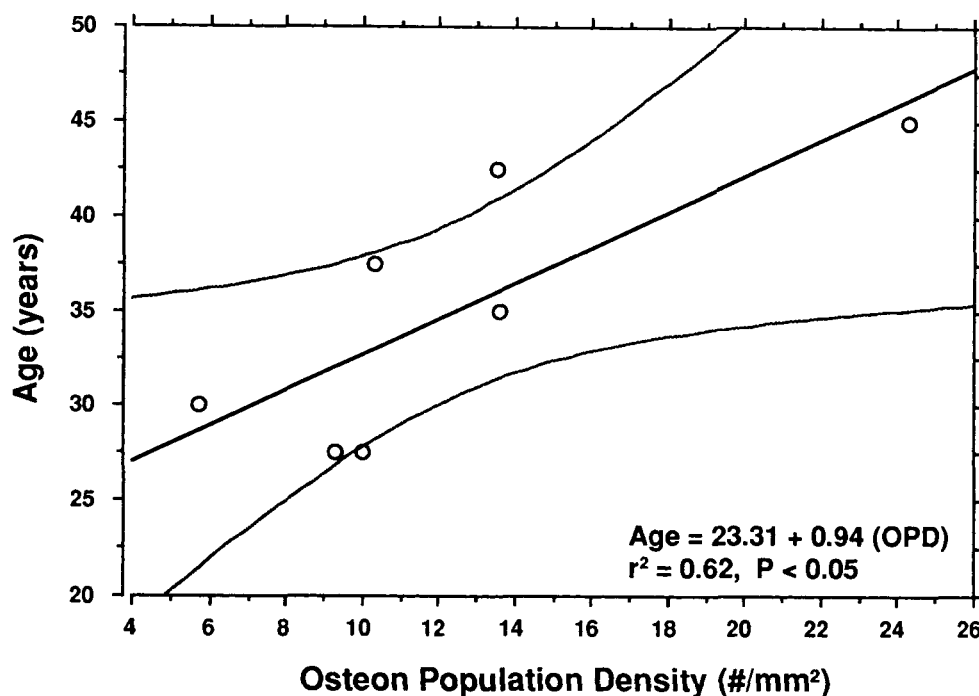


Fig. 2. Osteon population density was significantly correlated to morphological age ($P < 0.05$), as expected since osteons tend to accumulate with age. Using this regression, the Shanidar 2 specimen was about 34 years of age at death. Curved lines represent the 95% confidence intervals.

TABLE 4. Osteonal dimensions

Specimen	On.Ar (μm^2)	On.Pm (μm)	W.Wi (μm)	Ca.Ar (μm^2)	Ca.Pm (μm)	On.B (%)	Po (%)	On.Rf (%)	OPD ¹ (/mm ²)
Late Archaic									
Broken Hill	36277.47	696.62	74.36	3163.87	193.57	43.52	5.89	91.37	13.90
Shanidar 2	37575.38	707.33	78.82	2535.78	181.02	38.73	5.88	93.27	11.46
Shanidar 3	17725.87	486.23	55.36	1079.00	115.21	34.63	5.73	93.91	24.29
Shanidar 4	29767.66	634.78	65.20	2992.77	185.35	25.38	5.60	90.11	10.34
Shanidar 5	24292.44	573.48	64.49	1448.08	134.81	27.25	4.98	94.03	13.51
Shanidar 6	23033.76	564.10	62.13	1363.62	131.78	18.45	3.39	94.02	10.05
Tabun	29985.60	627.21	68.80	2305.11	170.93	22.85	3.37	92.26	9.29
Mean	28379.74	612.82	67.02	2126.89	158.95	30.12	4.98	92.71	13.26
SE	2516.19	27.33	2.73	291.56	10.84	3.15	0.40	0.53	1.81
Early Modern									
Skhul 3	16293.57	466.90	47.91	1589.10	146.94	11.33	3.24	90.25	8.02
Skhul 6	39287.42	756.00	74.44	3190.18	213.89	20.52	3.09	91.88	5.70
Skhul 7	22851.36	545.42	62.52	1456.14	139.03	25.08	3.46	93.63	13.61
Mean	26144.12	589.44	61.62	2078.47	166.62	18.98	3.26	91.92	9.11
SE	588.92	70.47	6.26	454.93	19.39	3.30	0.09	0.80	1.92
Group mean	27709.05	605.81	65.40	2112.36	161.25	26.77	4.46	92.47	12.02
Group SE	2452.24	28.71	2.79	245.62	9.63	2.87	0.39	0.48	1.51

¹Includes whole and fragmentary secondary osteons.

37.31 ± 3.23 years, $P = 0.06$). In particular, the Late Archaic sample demonstrates somewhat greater values for percent osteonal bone (Table 4, $P = 0.06$), and variables

related to osteon population density (OPD and AOC, $P = 0.13$). Because each osteon is associated with an Haversian canal, the greater number of osteons in the Archaic

TABLE 5. Dynamic bone remodeling factors

	OPD asymptote (mm ²)	OPD/OPD asymptote [α]	Scaling operator [β]	AOC ¹ (no./mm ²)	Net remod. ² (mm ²)	Ac.F ³ (no./mm ² /yr)	BFR ³ (%/yr)	Calculated age (yr)
Late Archaic								
Broken Hill	29.88	0.47	1.08	15.01	0.54	—	—	51
Shanidar 2	28.84	0.40	1.04	11.92	0.45	0.93	3.57	55
Shanidar 3	61.15	0.40	1.04	25.26	0.45	0.78	1.38	42
Shanidar 4	36.41	0.28	1.01	10.44	0.31	0.42	1.25	33
Shanidar 5	44.62	0.30	1.01	13.65	0.33	0.46	1.12	34
Shanidar 6	47.06	0.21	1.00	10.05	0.23	0.67	1.54	25
Tabun	36.15	0.26	1.01	9.38	0.28	0.63	1.89	30
Mean	40.59	0.33	1.03	13.67	0.37	0.65	1.79	39
SE	3.97	0.03	0.01	1.92	0.04	0.07	0.34	4
Early Modern								
Skhul 3	66.52	0.12	1.00	8.02	0.13	—	—	18
Skhul 6	27.59	0.21	1.00	5.70	0.22	0.33	1.30	28
Skhul 7	47.43	0.29	1.01	13.75	0.31	0.61	1.39	32
Mean	47.18	0.21	1.00	9.16	0.22	0.47	1.35	26
SE	9.18	0.04	0.00	1.95	0.04	0.10	0.03	3
Group mean	42.57	0.29	1.02	12.32	0.33	0.61	1.68	35
Group SE	4.02	0.03	0.00	1.61	0.04	0.07	0.26	3

¹ Accumulated osteon creations (AOC) = $\beta \times \text{OPD}$.

² Net remodeling (BR_n) = $\text{AOC} \times \text{On.Ar.}$

³ Ac.F and BFR calculated using macroscopically derived ages.

group translates into a higher porosity in this group as well.

Comparison of Pleistocene and Recent diaphyseal histology

Table 6 compares mean histologic and remodeling parameters in the Recent population and in the Late Archaic and Early Modern groups. These data show that the Pleistocene groups had significantly smaller osteons (Archaic vs. Recent females, $P = 0.003$; pooled sample vs. Recent, $P = 0.007$) and fewer of them (Archaic vs. Recent, $P < 0.005$; Modern vs. Recent, $P < 0.02$; for the pooled population, $P = 0.003$) than the more recent Pecos population. However, porosity was three times greater in the Pleistocene groups (Archaic vs. Recent, $P < 0.001$; for the pooled population, $P = 0.0001$), suggesting a greater number of primary vascular channels, and perhaps primary osteons. Even so, porosity in the Pleistocene groups is well within the normal range for cortical bone for modern EuroAmerican populations. On average, osteons are about 25% smaller in the Pleistocene populations than in more modern humans. Moreover, the Pleistocene hominids had about half as many intact secondary osteons as similarly aged but more modern individuals.

Osteon population density reflects the time-adjusted activity of bone remodeling, as osteons tend to accumulate with age. The smaller OPD therefore is consistent with the significantly lower activation frequency (Archaic vs. Recent, $P < 0.001$; Modern vs. Recent, $P = 0.03$; for the pooled population, $P = 0.0003$). The low relative activation frequency in turn contributes to the significantly lower relative bone formation rates in the Pleistocene populations (Archaic vs. Recent, $P = 0.001$; Modern vs. Recent, $P = 0.03$; for the pooled population, $P = 0.0003$). Activation frequency in the Pleistocene populations is about half that in more Recent groups, while the bone formation rate is only about one-third of that in the Pecos population.

DISCUSSION

All histological samples were partial cross sections or fragments except for the Broken Hill specimen. The latter consisted of an entire cross section, which was measured in two separate regions of the cortex. By necessity, histological samples were taken from different locations within the femur. Some control was exercised by limiting samples to the middle third of the femur, but the cortex from which the sample came varied. Consid-

TABLE 6. Mean histologic parameters¹

	Pecos/M 20-50	Pecos/F 20-50	Late Archaic 25-51	Early Modern 18-32	Late Pleis. (pooled) 18-51	P values ²				
						Archaic vs. Pecos	Vs.	Modern vs. Pecos	Vs.	Pooled vs. Pecos
On.Ar (μm^2)	35288.95 (2170.9)	41046.65 (2299.93)	28379.71 (2717.73)	26144.00 (6838.67)	27709.05 (2584.82)	0.003 NS	F M	NS		0.007
Ca.Ar (μm^2)	2267.55 (160.08)	2331.55 (184.43)	2127.00 (314.94)	2078.33 (557.16)	2112.36 (258.91)	NS		NS		NS
Ca.Pm (μm)	162.35 (4.91)	165.67 (6.09)	158.95 (11.71)	166.62 (23.75)	161.25 (10.15)	NS		NS		NS
On.Pm (μm)	678.14 (20.10)	734.11 (20.91)	612.82 (29.52)	589.45 (86.30)	605.81 (30.26)	0.003 NS	F M	NS		0.009
W.Wi (μm)	77.17 (2.81)	84.90 (2.82)	67.02 (2.95)	61.62 (7.67)	65.40 (2.94)	0.015 NS	F M	NS		0.003
On.Rf (%)	93.39 (0.34)	94.14 (0.47)	92.71 (0.58)	91.92 (0.98)	92.47 (0.48)	NS		NS		0.042
OPD ³ (/mm ²)	7.26 (0.33)	6.21 (0.34)	3.57 (0.40)	2.90 (0.52)	3.37 (0.32)	0.004 0.001	F M	0.016 0.013	F M	0.003
On.B (%)	25.01 (1.47)	25.19 (1.72)	30.12 (3.41)	18.98 (4.04)	26.77 (3.06)	NS		NS		NS
Po (%)	1.62 (0.12)	1.44 (0.13)	4.98 (0.43)	3.26 (0.11)	4.46 (0.39)	0.0005 0.0005	F M	NS		0.0001
Rel.Ac.F ⁴ (no./mm ² /yr)	0.22 (0.01)	0.20 (0.02)	0.10 (0.00)	0.09 (0.02)	0.10 (0.00)	0.01 0.002	F M	NS 0.04	F M	0.0003
Rel.BFR ⁴ (%/yr)	0.78 (0.07)	0.82 (0.07)	0.24 (0.01)	0.27 (0.01)	0.25 (0.01)	0.003 0.005	F M	NS NS	F M	0.0003

¹Standard errors in parentheses.²Kruska-Wallis one-way ANOVA followed by Dunn's nonparametric multiple comparison test.³Includes only whole secondary osteons.⁴Relative activation frequency and bone formation rate. Fragmentary osteons were not counted in the work on Pecos by Burr et al. (1990). Therefore, for comparative purposes Late Archaic and Early Modern populations' relative BFRs, were calculated using only whole secondary osteons. These values vary slightly from those in Table 5.

erable variability in morphology and remodeling dynamics occurs at different locations within a single bone (Stout, 1984). This affects both the age estimations (although these appear quite consistent with previous estimates, where known, Table 1) and the comparability of remodeling data among the different groups (Late Archaic, Early Modern, and Pecos). Because of this, the data should be interpreted with some caution. The rarity of the material prevents normal controls on sample location, but even without more rigorous control over sample location, the data are both informative and significant.

The histologically calculated ages at death resulting from this study confirm previous estimates of the Shanidar, Skhul and Tabun material (Table 1; McCown and Keith, 1939; Trinkaus, 1983; Trinkaus and Thompson, 1987). Our results demonstrate that histologic techniques constitute a valid method for estimating age from fragmentary fossilized cortical material, even when the quality of the material is variable.

While our calculated ages generally corroborate both the morphologically determined ages and the histologic ages previously calculated, our calculated age for Shanidar 2 is considerably older than the estimate made by Trinkaus (1983). This is also the only specimen that included only tibial cortical bone, which may account for the difference. The age calculation is based on the percentage of cortex that is remodeled, rather than on the number of osteons (OPD). The percentage of remodeled cortex in Shanidar 2 is nearly 3 standard deviations ($z = 2.75$) from the mean of the Archaic group. The large proportion of remodeled cortex is a function of the excavation and subsequent formation of very large osteons ($z = 3.65$ from the Archaic mean for On.Ar) with normal refilling (Table 4). This indicates that the activity of both osteoclasts and osteoblasts in this individual was increased above normal, although the balance between resorption and formation, and the number of remodeling sites (viz. OPD and Ac.F) was not disturbed.

Similar conclusions could be drawn for the Broken Hill individual, in which macroscopic ages are not available for comparison. The percent of remodeled cortex in the Broken Hill individual is more than 4 standard deviations above its group mean ($z = 4.25$, Table 4). Again, this is the result of osteons that are larger than average for the Late Archaic group ($z = 3.14$). Nevertheless, osteon size in both Broken Hill and Shanidar 2 is well within the modern range. (Table 6).

Within the 20–50 year age range, the dynamics of bone remodeling within the subsamples of the Pleistocene group (Archaic and Early Modern) are nearly identical. Remodeling in the Pleistocene group is quite similar, although not identical, to that in the Recent population. The most significant difference between Pleistocene and Recent populations is that bone turnover in the Late Archaic and Early Modern groups was significantly slower than in the Recent group. This is reflected in the smaller OPD, and the lower Ac.F and BFR.

Osteon size is smaller, indicating less vigorous osteoclastic activity at the level of the individual cell. However, the normal balance between bone formation and bone resorption was maintained. Osteoblasts replaced about 92% of the bone that was removed by osteoclastic action at any single location, while in the Pecos population osteoblasts replaced 93–94% (Table 6). These slight differences between Pleistocene and Recent populations were not statistically significant and in any case do not explain the higher bone mass in the Late Archaic and Early Modern populations. These observations indicate 1) that resorption and formation were both coupled and balanced in these Pleistocene populations and 2) that overall vigor of individual cells from both the osteoclast and osteoblast lines was probably somewhat less than in Recent populations. Cell vigor is a product of both the rate of activity (either formation or resorption) and the duration of that activity (Burr and Martin, 1989). Reduced cell vigor indicates either that the cells performed their work at a slower pace or that they did not survive as long as in Recent populations. These differences have no effect on the health of the bone in the absence of an imbalance between resorption and forma-

tion, but do indicate an overall lower metabolic rate for skeletal remodeling.

These observations in the later Pleistocene populations are all consistent with a skeletal structure placed under very high loads. According to Frost (1987c; Martin and Burr, 1989) higher strains will depress bone remodeling but stimulate bone modeling. Modeling adds bone to periosteal surfaces and prevents the expansion of the marrow cavity. Following on this, the robustness of the Pleistocene hominid skeletons can be explained by very active modeling during growth and development in response to large loads imposing high bone strains. High strains during adult life tend to depress bone remodeling, reducing the osteon population density. This predicted outcome can be observed in the Pleistocene group.

These differences with more recent populations in dynamic bone remodeling processes, while small, can be attributed to differences in load bearing. However, it is also true that a decrease in the threshold strain (what Frost (1987c, 1992) calls the setpoint) required to initiate bone remodeling could produce similar morphology. Bone normally operates within a physiologic range of mechanical strains (Burr and Martin, 1989). When the upper threshold strain is exceeded, bone will attempt to adapt through net bone formation, resulting in increased mass (Frost, 1987c; Martin and Burr, 1989). The range may be exceeded either because loads are large, or because the upper physiologic limit, which presumably is genetically set and metabolically maintained, is low. The bone will adapt in identical ways to increased strain and to decreased setpoint. The techniques used here to quantify dynamic bone remodeling cannot differentiate between them. Therefore, in explaining differences in remodeling rates between Pleistocene populations and more recent groups, we cannot exclude underlying fundamental differences in the genetically determined or physiologically regulated setpoints for bone response. In addition to these effects of habitual strain levels on osteonal dimensions, relatively small osteonal dimensions have been correlated with high levels of dietary and epidemiological stress. In particular, Van Gerven found significantly smaller os-

teon diameters (yet still larger than those observed here for these Pleistocene humans) in a sample of Medieval Nubians known from historical and other skeletal biological indicators (Van Gerven et al., 1990) to have undergone severe stress compared to later populations in the region. Although there is little evidence for epidemiological stress among these Pleistocene human groups, there is evidence for consistently elevated levels of nutritional stress among at least the Late Archaic humans, as indicated by their high frequency of dental hypoplasias (Ogilvie et al., 1989). To the extent discernable given dental occlusal attrition in the older individuals, all of the Near Eastern Late Archaic humans examined here exhibit multiple lesions indicative of high levels of dietary stress (comparable data are currently unavailable for the Skhul sample). It is therefore possible that the relatively small osteonal dimensions seen in these Pleistocene humans are a product of their highly stressful lives in combination with the elevated strain levels discussed above.

It is not possible to determine whether the histological differences between these Pleistocene human samples and Recent humans were primarily, or exclusively, the products of contrast in habitual systemic stress levels or biomechanical strains, and within the latter whether the differences resulted from increased load bearing or reduced setpoints. It is nonetheless clear that bone turnover and individual bone cell activity in Late Pleistocene populations were depressed relative to more recent humans.

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